Localization of tree water uptake in Scots pine and Norway spruce with hydrological tracers

Kevin Bishop and Etienne Dambrine

Abstract: This study explores the potential of hydrological tracers for determining the proportion of water uptake by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) from different layers in the upper 3 dm of podzolized forest soil. To improve the resolution of the tracer technique, a pair of tracers was employed. One tracer was the naturally occurring vertical gradient in the oxygen isotope ratio, $\delta^{18}O$, of soil solution. The second tracer was a ^{3}H solution placed in the mor layer. A three-component mixing model of water uptake was used to simulate the content of these two tracers in the xylem sap. Each component in the mixing model represented a horizontal layer of soil with a characteristic composition of $\delta^{18}O$ and ^{3}H. Two stands were investigated. In both stands, the volume-weighted water uptake by Scots pine occurred at a depth of 8–17 cm in the upper B horizon. This was below the concentration of fine roots in the mor layer and the upper few centimeters of mineral soil. In one of the two study stands, Norway spruce was present. It had mean uptake depths ranging from within the mor layer to 5 cm below the mor–mineral soil contact. An uncertainty in the water uptake depth for each tree of ±1–2 cm was estimated from a Monte Carlo analysis of uncertainties in the model inputs. In addition to these specific results, the study demonstrated that isotopic tracers provide a simple and effective method for determining the vertical distribution of water uptake.

Résumé : Ce travail explore les potentialités qu'offrent les traceurs isotopiques classiquement utilisés en hydrologie pour déterminer la profondeur moyenne à laquelle les racines des arbres forestiers prélèvent leur eau d'alimentation. Dans deux placeaux forestiers du Nord de la Suède, dont une pinède (*Pinus sylvestris* L.) sur sol podzolique bien drainé et un peuplement mixte de pin et d'épicéa sur podzol ennoyé par une nappe à faible profondeur, nous avons mesuré les gradients naturels d'abondance isotopique en ^{18}O de l'eau dans le sol en fonction de la profondeur. Pour affiner le traçage, une faible quantité d'eau tritiée a été rajoutée en surface. Cinq jours après cet apport, les arbres ont été abattus et leur séve xylémique a été extraite de la base du tronc, par déplacement. La comparaison des valeurs d'abondance isotopique des sèves xylémiques et de celles mesurées dans les sols montre que les épicéas prélèvent en moyenne leur eau dans l'humus et l'horizon E, tandis que les pins s'alimentent préférentiellement dans l'horizon Bh. Cette différence est confirmée par les mesures d'activité spécifique en ^{3}H des sèves. On met ainsi en évidence une différence fonctionnelle préalablement établie sur des bases morphologiques et écophysiologiques, à savoir que l'enracinement des pins est plus profond que celui des épicéas. L'analyse des abondances isotopiques des sèves en fonction des circonférences à 1,3 m des arbres montre d'autre part que les arbres de plus faible biomasse s'alimentent à partir d'horizons plus superficiels que la moyenne. Cette technique apparait succeptible de développement intéressants dans le domaine des études de concurence interspécifique pour l'eau et les éléments minéraux, ainsi que pour interpréter les conséquences de divers stress sur l'alimentation d'arbres forestiers.

Received January 25, 1994. Accepted September 30, 1994.

K. Bishop.[1] Department of Forest Ecology, Faculty of Forestry, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
E. Dambrine. Centre de Recherches Forestières, Institut National de la Recherche Agronomique F-542 80 Champenoux, France.

[1] Author to whom all correspondence should be addressed.

Introduction

Forest soils often have distinct vertical gradients in their chemistry and water availability. This makes it interesting to know the uptake of water by trees from different levels in the soil profile. A limited number of studies have determined the distribution of water uptake from hydrometric measurements (Nnyamah and Black 1977; Garnier et al. 1986; Nordén 1989). The difficulty of making such

measurements, however, has often resulted in reliance on estimates of water uptake that could benefit from better information about the vertical distribution of water uptake. One example of where such information is critical is in the investigation of the interaction between drought and acidification (Dambrine et al. 1993).

A common method for estimating the distribution of water uptake is to assume that it is defined by the distribution of roots or a mathematical representation of that distribution (Jansson and Halldin 1980). This can be incorrect in some cases, because one of the findings from the handful of hydrometric studies of water uptake is that the vertical distribution of water uptake does not necessarily coincide with the distribution of roots (Nordén 1990). Trees can select the roots that are activated and discriminate between uptake of water and nutrients (Kramer and Bullock 1966; Caldwell 1976; Landsberg and McMurtrie 1984; Legge 1985).

Conservative hydrological tracers provide an alternative means of identifying the location of water uptake and can be applied more easily, and hence more regularly, than hydrometric studies. The potential of isotopes for distinguishing the sources of water uptake by trees is being increasingly recognized (White 1988; Ehleringer and Dawson 1992). The differences between oxygen and (or) hydrogen isotope ratios in groundwater and river water have already been used to identify the ratio of river water to groundwater taken up by riparian trees (Dawson and Ehleringer 1991; Rodelli et al. 1984; Thorburn et al. 1992). In those studies, the isotope ratios in xylem sap were treated as a mixture of two isotopically distinct components, river water and groundwater. Two-source mixing models have also been used to determine the contributions of recent rainwater and groundwater to tree uptake (White et al. 1985; Flanagan et al. 1992), as well as to document the hydraulic lift mechanism in some trees that transfer water from deeper to more superficial soil layers (Dawson 1993).

These previous studies have largely focused on the contribution to tree water uptake coming from a source external to the soil water, e.g., river water, rainwater, or deep groundwater. Such applications have not addressed the need for resolving the distribution of water uptake from different layers in the superficial soil horizons, where most nutrient cycling occurs in many forest ecosystems. The capability of distinguishing more than two sources of water uptake would also be desirable given the large variation in soil chemistry and biology that can occur within the rooting zone. The common reliance on a single independent tracer, though, has limited most previous studies to partitioning water uptake into just two components. The potential of using multiple hydrological tracers to improve the resolution of water uptake models was exploited by Walker and Richardson (1991) in a study of an irrigated *Pinus radiata* D. Don stand. Unfortunately, the uneven spread of the tracers introduced with the irrigation water complicated the interpretation of that experiment.

The conditions in forest soils are such that isotope techniques could help resolve the vertical distribution of water uptake in the rooting zone. Like many other features of soil solution, there can be a well-defined gradient in the naturally occurring stable isotope ratios of $\delta^{18}O$ and $\delta^{2}H$ within the soil (Bishop 1991). These gradients are markers that can help to resolve the locus of water uptake, and artificially introduced hydrological tracers can be used to complement that tracer signal, as Walker and Richardson (1991) demonstrated.

This study investigates the potential of using conservative hydrological tracers to define the vertical pattern of water uptake in the upper decimeters of the soil in two forest stands in northern Sweden. The study also seeks to demonstrate the power of using two independent hydrological tracers to increase the resolution of isotope techniques.

Experimental site

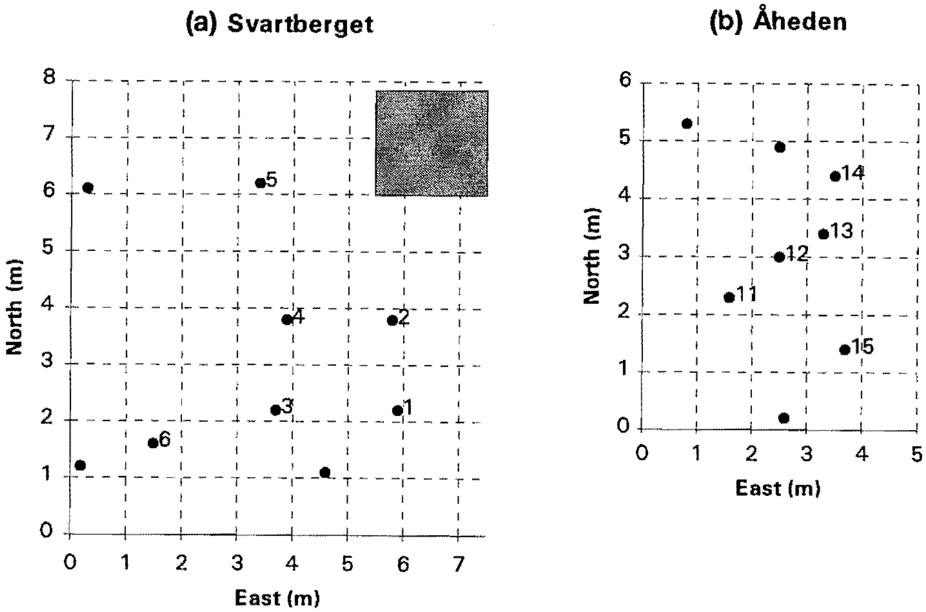
This experiment was conducted at two locations within the Svartberget Research Forest (64°14′N, 19°46′E) in northern Sweden, 60 km northwest of Umeå (Fig. 1). One of the sites, referred to as Svartberget, was a mixed stand of 55- to 75-year-old Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) growing at 260 m above sea level on the lower part of the east-facing slope of a blocky moraine deposit. The stand is in a vegetational transition zone between the upper slope (occupied by a Scots pine stand with a *Vaccinium myrtillus* understory on Ferric Podzols) and the bottom slope (where a Norway spruce stand grows on peaty Podzols with *Sphagnum* spp. present in the field layer). The Svartberget soil profile is a typical Humo-ferric Podzol. The mor layer was ca. 7 cm thick, and the bleached E horizon was also ca. 7 cm thick. This overlays a Bhs horizon that extended from 7 to 17 cm depth, albeit with large local variation. This is underlain by a Bs horizon. The silt and clay content is ca. 20% in the unsorted till soil. During the experiment, the water table was ca. 50 cm below the soil surface, as observed in an open drain beside the study site.

The second site, referred to as Åheden, was a 60- to 70-year-old Scots pine stand growing on a level, sandy, fluvial sediment 200 m above sea level where a weakly podzolized soil had developed. The field layer vegetation was dominated by *Vaccinium myrtillus*, *Vaccinium idaea*, and *Polytrichum* ssp. The soil profile at Åheden had a 2–3 cm mor layer overlaying an E horizon of similar thickness. The weakly developed Bhs horizon extended from ca. 3 to 10 cm depth. The texture of the entire profile was sandy, with less than 10% silt or clay except in lenses, where the fine content was higher. Groundwater was several meters below the soil surface.

Methods

Xylem sap consists of water taken up from the roots. It can be regarded as a mixture of water from several sources at different levels in the soil. If these sources have different compositions of hydrological tracers, then it is possible to resolve the vertical distribution of tree water uptake by means of a conceptual model of water uptake (Fig. 2). In this model, xylem sap in the tree bole is a product of water uptake from discrete horizontal layers in the soil, each with a unique composition of the isotopes which will be used as hydrological tracers.

Fig. 1. The plots treated with the ^{3}H tracer and the location of trees on those plots at Svartberget (*a*) and Åheden (*b*). Xylem sap was taken from the numbered trees. (See Table 1 for more information on each tree.) The roots were cut along the edge of each plot to a depth of 30 cm. Tritium tracer solution was not applied to the 4-m^2 area on the Svartberget plot, which is shaded.



The proportion of water taken up from each source layer is determined from a series of mass balance equations, the first being for the mass of water:

$$[1] \quad V_1 + V_2 + ... + V_n = V_{tot}$$

where V_{tot} is the total amount of water taken up by the tree and V_1 ... V_n represent the amount from each of n sources. Further mass balance equations can be written for each of p conservative tracers t_1, t_2, ..., t_p of water uptake:

$$[2] \quad C_1^{t_1}V_1 + C_2^{t_1}V_2 + ... + C_n^{t_1}V_n = \overline{C^{t_1}}V_{tot}$$

$$[3] \quad C_1^{t_2}V_1 + C_2^{t_2}V_2 + ... + C_n^{t_2}V_n = \overline{C^{t_2}}V_{tot}$$

where $C_1^{t_1}$ ... $C_n^{t_p}$ is the concentration of each tracer in each water source. (Conservative means that in a mixture of waters from sources with different tracer concentrations, the resulting tracer concentration is determined solely by the proportion of different sources in the mixture.)

With these equations, the proportion of water taken up from each source layer (V_n/V_{tot}) is uniquely determined for $n = p + 1$ sources, provided that the assumptions of the model are correct. With one hydrological tracer ($p = 1$) for the sources of xylem sap water, two mass balance equations can be written (eqs. 1 and 2), making it possible to uniquely determine the proportion of uptake from two sources. With a second tracer ($p = 2$), a third mass balance equation (eq. 3) can be written, and the uptake from three sources can be determined.

The basis for differentiating the sources of water uptake with hydrological tracers is the observation that the uptake of water does not fractionate either the oxygen or hydrogen isotope ratios in water (i.e., the isotope ratio in water taken into the root is identical with that in the water outside the root; Wershaw et al. 1966; Allison et al. 1984; Bariac et al. 1989; Thorburn et al. 1993). In this study, both the oxygen isotope ratios and a hydrogen isotope are used.

The oxygen isotope ratio in a sample, $\delta^{18}O$, is defined as the extent to which the ratio between ^{18}O and ^{16}O deviates from the ratio in the internationally accepted reference, standard mean ocean water (SMOW; eq. 4.).

$$[4] \quad {}^{18}O_{sample} = \frac{\left[\frac{^{18}O}{^{16}O}\right]_{sample} - \left[\frac{^{18}O}{^{16}O}\right]_{SMOW}}{\left[\frac{^{18}O}{^{16}O}\right]_{SMOW}}$$

This is not identical with a concentration, but can be treated as such in the range of deviations occurring in natural water (Craig 1961). The isotope ratio between ^{1}H and ^{2}H is also denoted as the relative deviation, $\delta^{2}H$, from a standard ratio.

The naturally occurring vertical gradients of soil water $\delta^{18}O$ and $\delta^{2}H$ can both be used as hydrological tracers. $\delta^{2}H$ and $\delta^{18}O$, however, have a strong correlation in precipitation that results from covariation in their fractionation during phase changes associated with the hydrological cycle (i.e., evaporation and condensation; Dansgaard 1964). Thus, these two tracers do not necessarily provide independent information about the sources of water uptake in the soil profile (cf. Walker and Richardson 1991; Thorburn and Walker 1993).

Therefore, to provide better resolution of water uptake sources, a second, independent hydrological tracer, ^{3}H (tritium), was used as a tracer added artificially to the soil profile. The content of the radioactive ^{3}H isotope in water is reported in bequerels (Bq), with 1 Bq being the concentration of a radioactive isotope that generates one radioactive

disintegration per second. Tritium is not a stable isotope, but since it has a half-life of 12.6 years, the changes in the concentration of ^{3}H due to radioactive decay during the two weeks of the experiment were negligible.

The concentration profiles of these tracers in soil solution were determined from soil solution samples extracted by centrifugation using the technique developed by Giesler and Lundström (1991). Volumetric moisture content in the soil was determined from intact soil samples dried for 24 h at 105°C.

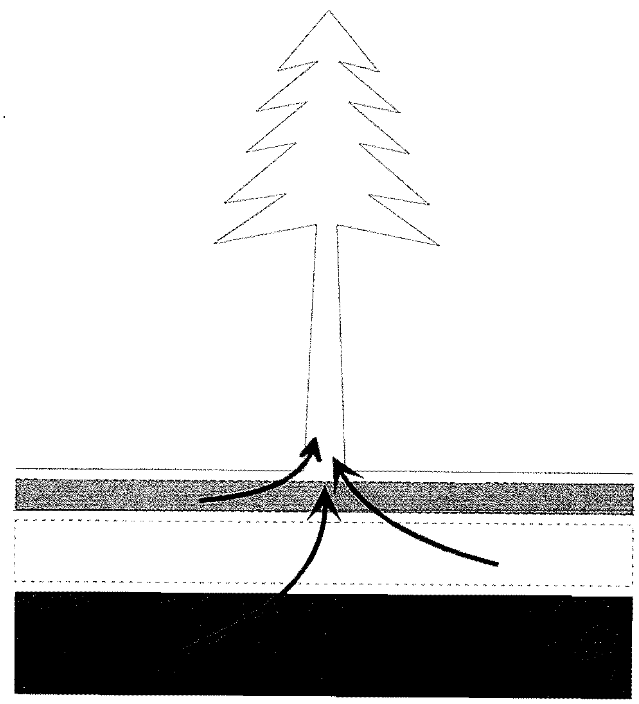
Samples of xylem sap water for determination of tracer concentrations were collected by extracting xylem sap from the tree using the displacement method described by Glavac et al. (1990). One meter long logs were cut from the bottom of the tree bole (0.5 to 1.5 m above ground level). A 10 cm wide band of the bark and underlying phloem were removed from both ends of each log to avoid the possibility of contaminating the xylem sap with fluid from the phloem. The logs were then positioned vertically, and a rubber sleeve (cut from an inner tube) was attached to the upper end of the log. Water was poured into the sleeve, where it formed a pool pressing down on the xylem sap in the log. A pool several centimeters deep provides sufficient pressure to displace xylem sap from the boles of many conifers. A dye was mixed with the water used to displace the xylem sap so that any leakage into the xylem sap would be apparent.

Concentrations of ^{3}H were measured at the Mass Spectrometry Laboratory of the Hydrology Division at Uppsala University using a Quantulus, low background, liquid scintillation spectrometer with an accuracy of better than ±100 Bq/L. At the same laboratory, a VG Isogas mass spectrometer was used to measure δ^{18}O with an accuracy of better than ±0.05‰.

The experiment began at the end of July 1990, when the ^{3}H tracer solution (ca. 0.37 GBq in 1 L of water per square meter of soil) was spread onto the F and H layers of the mor by lifting clumps of the litter layer of the mor, sprinkling the ^{3}H solution on the humus surface, and then replacing the clumps. The solution was spread over 28 m^2 at the Åheden site on July 26, 1991, and 56 m^2 at Svartberget on July 27 (Fig. 1). The roots crossing the boundary of the study plots were cut to a depth of 30 cm with a spade to ensure that the study trees transpired water from within the treated plot.

Most of the superficial root system lay beneath the litter layer, which was moved to apply the ^{3}H solution, so it is assumed that the function of the superficial root system was not significantly impaired. The application method can result in lateral variations in ^{3}H concentrations within every square meter of the study plot. Uptake by the root system is assumed to integrate those local differences within each soil layer to the average concentrations measured by the subsequent soil sampling for ^{3}H, which is described below. The addition of 1 L of water per square meter of study area, however, generates local increases in soil moisture content just where the ^{3}H is concentrated. Assuming that each liter of ^{3}H solution was absorbed by half of the soil surface to a depth of 5 cm, the volumetric concentration in the vicinity of the ^{3}H tracer solution would be increased by 4% from an initial moisture content of ca. 30% at Åheden and 35% at Svartberget. This may promote root activity in the vicinity of the ^{3}H, and thus tend to increase the water uptake from the superficial soil layer where the ^{3}H was applied.

Fig. 2. The conceptual mixing model of water uptake where the xylem sap is composed of water from several different sources, each of which is a horizontal layer of soil. For the mixing model to work, the concentration of one or more conservative hydrological tracers in each layer must be represented by a single value, and the tracer signature of each source must be distinct from those of the other sources.



Immediately after initiation of the ^{3}H at each site, plastic sheeting was spread on the soil surface to inhibit alteration of the tracer profile through either evaporation or percolation of subsequent precipitation. In the two weeks prior to the tracer experiment, 35 mm of rain had fallen. A further 2 mm fell during the experiment after the soil had been covered.

Five days after the ^{3}H marking of the soil profile, five Scots pines were felled at Åheden. At Svartberget, three Scots pines and three Norway spruce were felled (Table 1 and Fig. 1). One-meter lengths of trunk were cut and transported in plastic bags to the laboratory. Xylem sap was removed by pressure displacement from these sections. In each case, the first 100 mL of displaced xylem sap was discarded and the second 100 mL was collected for analysis. The data on xylem sap reported in this paper come from the basal section of trunk on each tree (0.5 to 1.5 m above ground level).

Potential evapotranspiration during the period of ^{3}H exposure was 26 mm at Åheden and 21 mm at Svartberget, as calculated by the method of Penman (1963). Actual evapotranspiration in this region during the summer is usually more than half of the potential evapotranspiration (Eriksson 1986). With such evapotranspiration rates, the

Table 1. The study trees.

Tree	Location	Species	Height (m)	Circumference at breast height (cm)	Age (years)
1	Svartberget	*Pinus sylvestris*	13.7	53.0	59
3	Svartberget	*Pinus sylvestris*	16.0	64.0	57
4	Svartberget	*Pinus sylvestris*	12.6	40.5	65
2	Svartberget	*Picea abies*	15.2	52.5	77
5	Svartberget	*Picea abies*	12.5	52.0	95
6	Svartberget	*Picea abies*	12.0	40.5	60
11	Åheden	*Pinus sylvestris*	12.0	45.0	60
12	Åheden	*Pinus sylvestris*	11.0	27.0	58
13	Åheden	*Pinus sylvestris*	11.1	35.0	66
14	Åheden	*Pinus sylvestris*	10.3	43.0	65
15	Åheden	*Pinus sylvestris*	12.3	41.0	68

area of each study site, and the number of trees on each site, an average of more than 40 L was transpired by each tree after the ^3H application at Åheden and 60 L per tree at Svartberget. Given a water content of ca. 50% in the sapwood and assuming that the entire trunk is sapwood, although ca. one-third is not likely to be sapwood (Granier et al. 1995; Lu et al. 1995), the amount of water in each tree between ground level and a height of 1.5 m in the bole varies from 5 L for the smallest tree (28 cm circumference at breast height (CBH) to 12 L in the largest tree at Åheden (45 cm CBH) and 25 L in the largest tree at Svartberget (65 cm CBH). Thus, even allowing for water held below ground level in the root system, but not accounting for the fact that larger trees will transpire a larger proportion of the transpiration from each study plot, it can be assumed that the water in the xylem sap at the base of the bole was taken up from the soil after the ^3H injections.

On the same day as the trees were felled, and immediately after the removal of the plastic ground cover, three bulk soil samples were taken from each study plot to determine the disposition of the ^3H layer at the surface of the soil profile. At Åheden, those samples were taken from the mor, 0–10 cm, and 10–20 cm depths. At Svartberget, the samples were taken from the mor, the E horizon (0–7 cm), and the B horizon (7–30 cm). The bulk sample from each horizon was the result of ca. 50 individual 500-cm^3 samples. Three replicate samples of soil solution were centrifuged from each of the bulk soil samples for ^3H analysis. The profile of $\delta^{18}O$ in the soil had been sampled prior to the addition of the ^3H tracer by collecting 5 L of soil from consecutive 5–10 cm layers along a 1-m face of a sampling pit dug on each study site.

Results

The ^3H concentration in soil solution at Svartberget ranged from 1500 to 3200 Bq/L in the replicate samples of soil solution from the mor layer to less than 100 Bq/L below a depth of 10 cm in the mineral soil (Fig. 3*a*). At Åheden, the ^3H concentration ranged from 4000 to 6000 Bq/L in the mor and uppermost centimeters of the mineral soil to between 600 and 1200 Bq/L in the second decimeter of the soil profile (Fig. 3*b*). At Svartberget, where the mor layer was thicker and the soil moisture content was higher, the ^3H was more dilute and was retained in the mor longer than at Åheden, where the mor was thinner and the soil moisture content was lower.

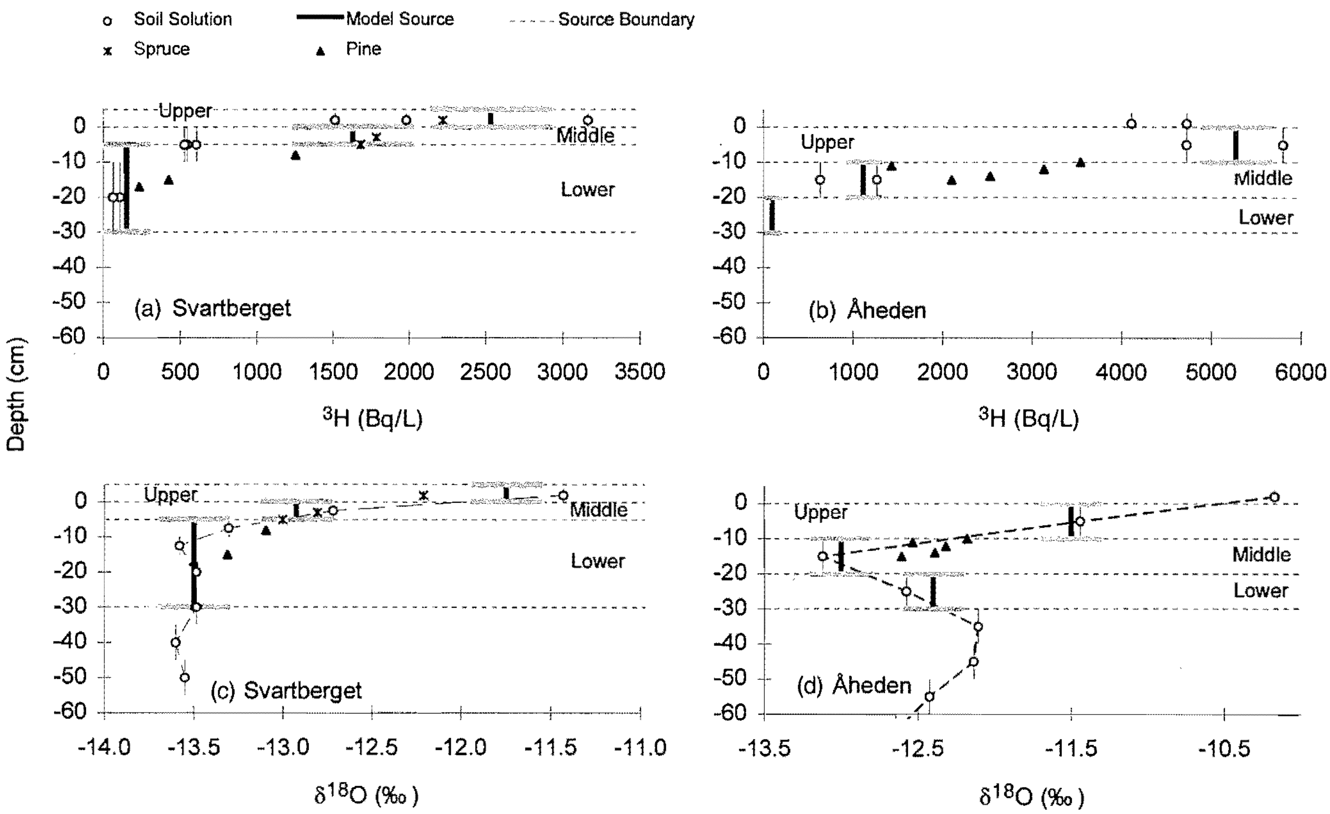
The soil water in the mor layer of both sites was strongly enriched with the heavier ^{18}O isotope, yielding a $\delta^{18}O$ value of −11.4‰ at Svartberget (Fig. 3*c*) and −10.3‰ at Åheden (Fig. 3*d*). This vertical pattern of $\delta^{18}O$ is consistent with enrichment of the superficial soil solution by evaporation from the ground surface, which preferentially leaves the heavier isotope in the liquid phase. The pattern of superficially enriched $\delta^{18}O$ could be reinforced by inputs of summer precipitation, which are more enriched in ^{18}O than witner and spring precipitation.

At Svartberget, the $\delta^{18}O$ value in the soil solution declines down through the mor and E horizon to a value of −13.5‰ in the B horizon (30 cm depth), below which the $\delta^{18}O$ remains relatively constant (Fig. 3*c*). This homogeneity is influenced by the presence of a fluctuating water table in the B horizon. At the time of this experiment, the groundwater level in the study site was at 50 cm depth. On the basis of measurements in plots within 100 m of the study site, the groundwater level varies between ca. 30 and 100 cm depth. That large reservoir of water and its movement can dampen out the natural variation, both seasonal and short term, in the $\delta^{18}O$ of precipitation.

At Åheden, the profile of $\delta^{18}O$ in soil solution decreases from −10.3‰ down to −13.3‰ at 15 cm depth, then increases to −12.1‰ at 35 cm depth, before decreasing again (Fig. 3*d*). This vertical pattern can better reflect the $\delta^{18}O$ of successive precipitation events (Saxena 1987) because the water table lies several meters below the ground surface and is not in connection with the root system of the trees.

The $\delta^{18}O$ in the xylem sap of Scots pine at Svartberget ranged from −13.0 to −13.5‰, and the ^3H concentration was between 200 and 1400 Bq/L (Figs. 3*a* and 3*c*). The

Fig. 3. Values of ^3H concentration at different depths in the soil profiles at Svartberget (*a*) and Åheden (*b*), as well as $\delta^{18}O$ values in those profiles (*c* and *d*). The vertical extent of the line through each soil solution value represents the thickness of the soil layer from which the soil solution was extracted. The content of each tracer in the xylem sap of each tree sampled is shown for comparison. The xylem sap values are plotted at the volume-weighted mean depth of water uptake for each tree as calculated in Fig. 6 from the three-source mixing model. The vertical extent of each soil water source and the tracer value assigned to that source are superimposed on the diagram as thick vertical lines. The subjectively determined uncertainty in the isotope composition of the water sources is represented by the horizontal extent of the shaded lines bounding each water source.



Norway spruce, present only at Svartberget, had distinctly different values of xylem sap $\delta^{18}O$, which ranged from −12.2 to −12.9‰, and higher ^3H concentrations, from 1700 to 2300 Bq/L. At Åheden, the $\delta^{18}O$ of xylem sap in Scots pine was between −12.1 and −12.8‰, with ^3H concentrations in the range of 1200 to 3600 Bq/L (Figs. 3*b* and 3*d*).

Discussion

Comparison of the isotope tracer values in xylem sap and soil solution (Fig. 3) suggests that most water uptake by Scots pine occurs below the mor layer even though the root biomass was concentrated at the soil surface on these study sites (Nordén 1989). Norway spruce, on the other hand, appears to take up water more superficially, closer to the mor layer. This difference in vertical patterns of water uptake by Norway spruce and Scots pine was quantified with the mixing model of water uptake.

To implement the three-source mixing model of water uptake, the soil solution profiles of ^3H and $\delta^{18}O$ were separated by visual inspection into three potential water sources. Each source represents a horizontal layer in the soil assumed to have a uniform concentration of $\delta^{18}O$ and ^3H (Fig. 3). The uncertainty in the isotopic composition assigned to each water source was estimated subjectively to 0.2‰ for the value of $\delta^{18}O$ (Figs. 3 and 4) and 500 Bq/L for ^3H (with the exception of the lower source areas, which had an uncertainty of 100 Bq/L). The respective uncertainties in the measurements of xylem sap ^3H and $\delta^{18}O$ were conservatively assumed to be ±100 Bq/L and ±0.05‰ (Fig. 4).

Groundwater was not treated as a distinct source of water, as it has been in some other studies. At Åheden the water table is too deep to be in contact with the root system. At Svartberget transient saturation of the soil between 30 and 100 cm depth makes the definition of "groundwater" at a particular level ambiguous. Furthermore, since shallow groundwater is not isotopically distinct from soil solution in the unsaturated soil below 30 cm depth, groundwater could not be distinguished from soil water on the basis of its isotopic content.

The mixtures of xylem sap that can be created by uptake from these three water sources are represented in a mixing diagram for $\delta^{18}O$ and ^3H (Fig. 4). Xylem sap tracer concentrations that lie within the triangular "water source space" defined by the tracer content of the potential water sources can be generated by chemically conservative mixing in portions uniquely determined by eqs. 1–3 (Fig. 5). In those cases where the xylem sap lies outside the water source space, and the model cannot reproduce the xylem sap concentrations, the uptake from the potential sources was

Fig. 4. The $\delta^{18}O$ and ^{3}H tracer contents of the three potential soil solution sources of tree water uptake at Svartberget (*a*) and Åheden (*b*). The tracer signature of these potential sources define a triangular region. This region delimits the range of xylem sap tracer contents that can be produced by mixing the three soil solution sources. The measured xylem sap concentrations are also plotted. The uncertainty in the isotopic analysis of each xylem sap isotope value and the water sources of the mixing models are represented by error bars. Symbols are as defined in Fig. 3.

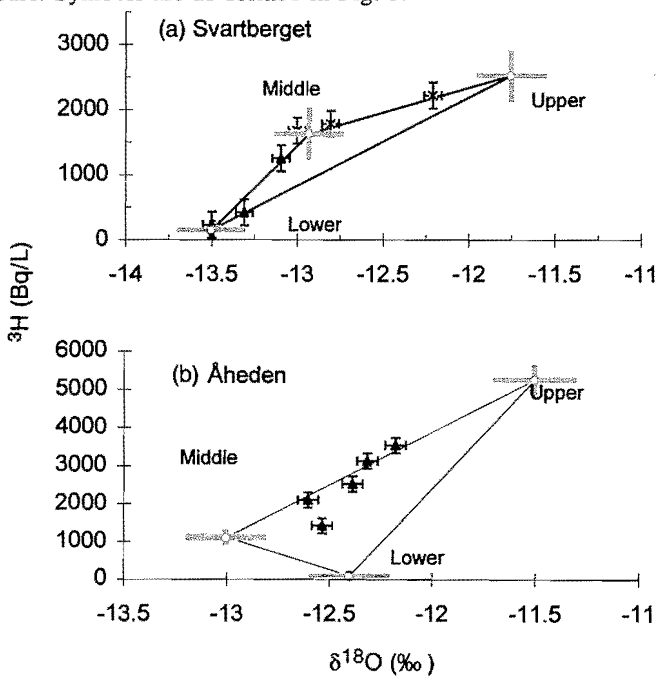
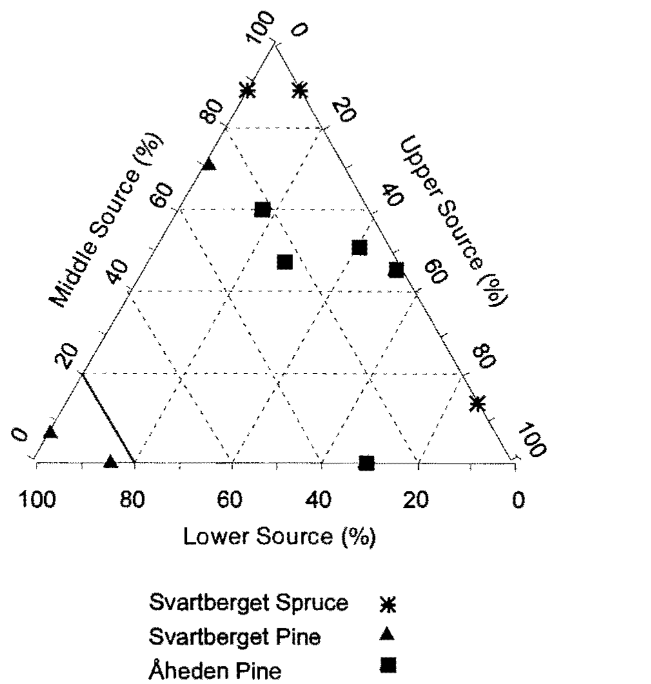


Fig. 5. Triangular mixing diagram of the proportion of water taken up from each of the three potential sources of soil solution according to the mixing model defined using eqs. 1–3. In those cases where the xylem sap values lie outside the region that can be simulated by the model, the proportions of uptake from each water source have been chosen to minimize the error in tracer content predicted by the model.



calculated to minimize the square of the difference in deviation of the predicted $\delta^{18}O$ and ^{3}H values from the observed values. The most likely sources of error that result in xylem sap values lying outside the water source space are uncertainties in the definition of the potential water sources, with respect to their number, location, or isotopic composition.

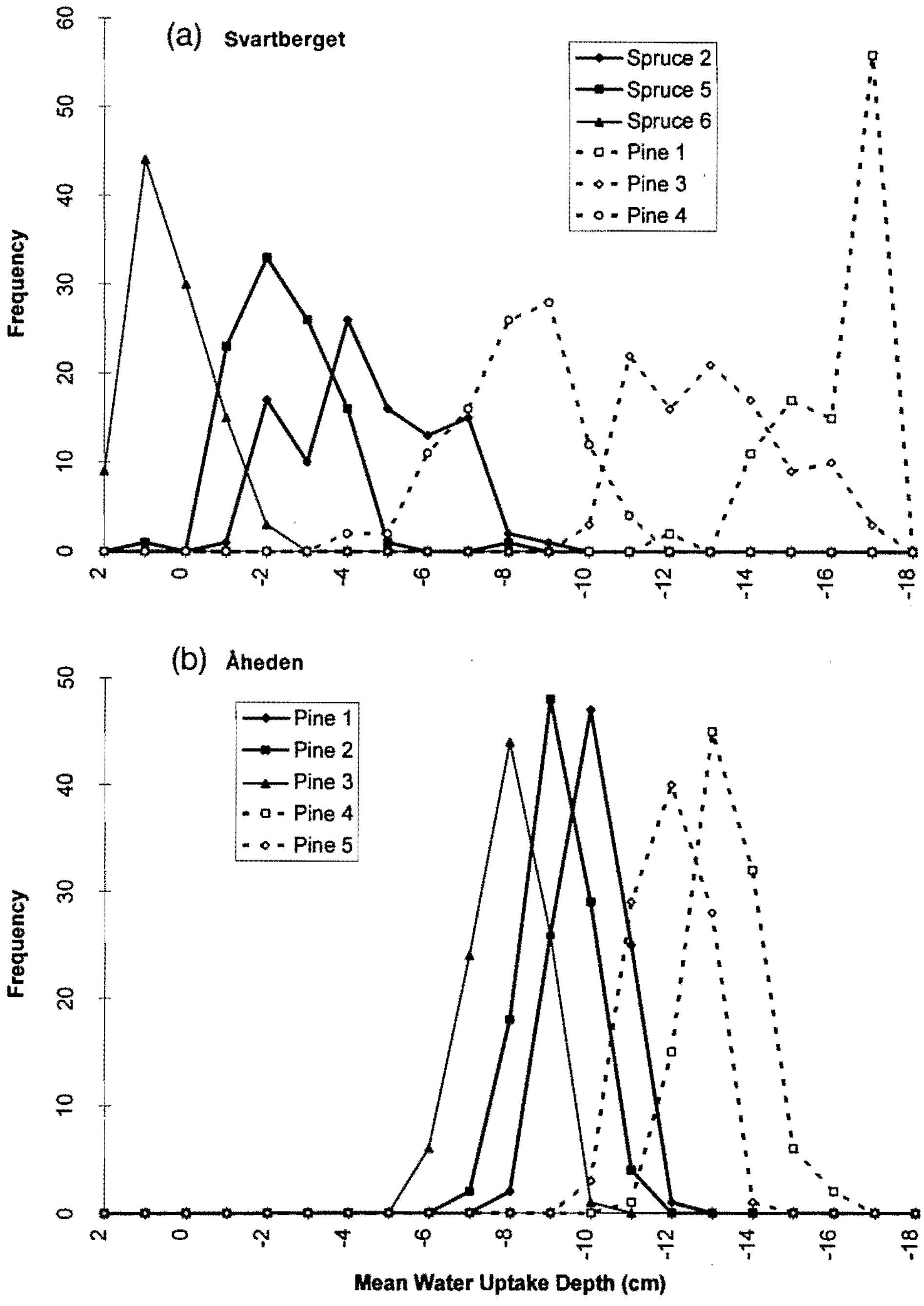
To assess the effect of uncertainty in the definition of the isotopic composition of the three model water sources, as well as analytical uncertainties in the xylem sap isotope analyses, Monte Carlo simulation was used. In this approach, 100 values of the $\delta^{18}O$ and ^{3}H in each of the modeled water sources and the xylem sap analyses were selected at random, with uniform probability, from within the uncertainty range for each isotope value. The three-component water uptake model was then applied to each of the 100 randomized combinations of source water and xylem sap compositions. The volume-weighted mean uptake depth for each combination was then calculated from the mean depth of each water source and the proportion of water taken up from that source. This yielded a distribution of volume-weighted mean water uptake depths for each tree that reflects the effect of uncertainty in definition of the water sources and isotope analyses (Fig. 6).

A volume-weighted mean depth of water uptake for each tree was calculated both from the estimated isotopic composition of the water uptake sources and from the average values of the 100 Monte Carlo simulations. These two uptake depths could differ by up to 2 cm, but the 100 estimates of mean water uptake depths in the Monte Carlo simulation for each tree had standard deviations of less than 2 cm. This range of uncertainty was not large enough to obscure clear differences in the depth of water uptake for pine and spruce (Fig. 7).

The average depth of water uptake by the different Norway spruce trees at Svartberget was 3 cm, while for Scots pine the average uptake depth was 13 cm at Svartberget and 11 cm at Åheden. The deeper uptake of water by Scots pine relative to Norway spruce has long been accepted on the basis of differences in rooting morphology (Kostler et al. 1968), but this study provides functional evidence of that difference.

At both Åheden and Svartberget, the bulk of root biomass, including Scots pine roots, are located in the mor horizon (Nordén 1989). This is consistent with investigations of conifer rooting in Sweden which have shown that more than 70% of the fine-root biomass in the upper 30 cm of soils is located in the mor layer (Majdi and Persson 1993). A similar distribution has been reported in other boreal forests (Kimmins and Hawkes 1978). Thus, this study confirmed the ability of Scots pine to differentiate water uptake from its root system to such a degree that most of the water is not taken up in the mor layer where most of the roots are located, even though the mor was moist. These results are all the more striking in light of the fact that

Fig. 6. The distribution of 100 Monte Carlo estimates of the volume-weighted mean water uptake depth for each tree at Svartberget (*a*) and Åheden (*b*). In these analyses, the isotope values for ^3H and $\delta^{18}O$ in the model water sources were selected randomly, with uniform probability, from within the range of uncertainty for the definition of the water source isotope compositions (cf. Fig. 3) and the analytical uncertainties in the analyses of xylem sap isotope values.

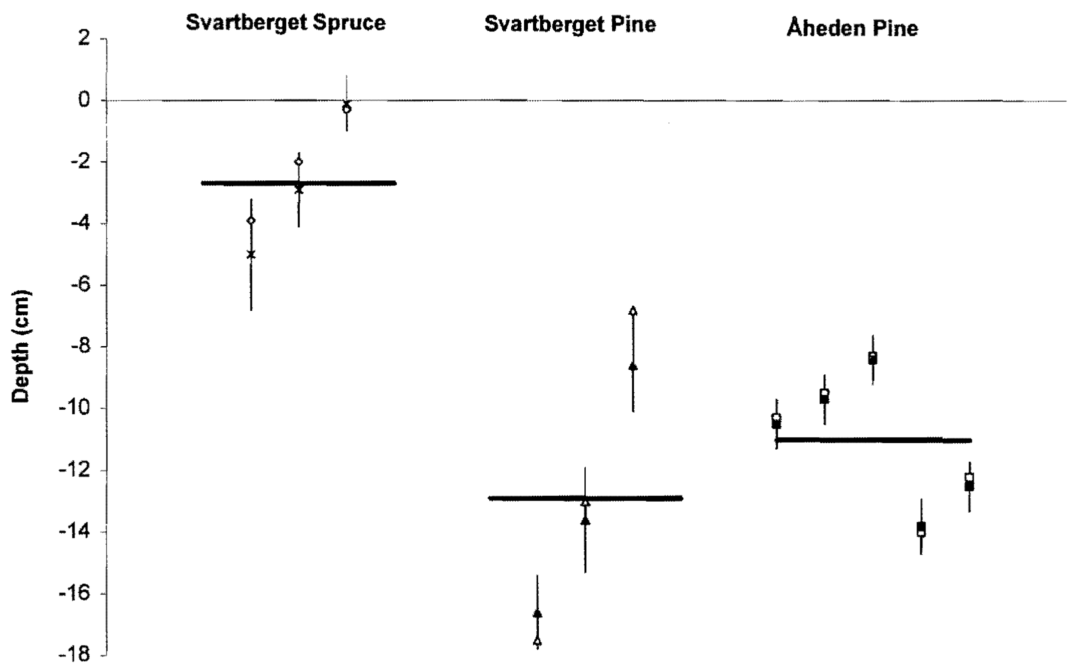


the application of ^3H solution to the superficial soil layer increased the moisture content where the ^3H was concentrated. The likely effect of this superficial "irrigation" is to promote uptake of ^3H. This would result in an overestimate of the uptake of water by superficial roots.

Within each tree species and on each site, there is a tendency for tree height and CBH to be related to a deeper mean level of water uptake (Fig. 8). As in the case of Scots pine versus Norway spruce water uptake depths, the relationship between water uptake depth and tree biomass is not surprising. The key to this finding is the demonstration of another facet of the information that hydrological tracers in xylem sap can provide for testing ecological hypotheses.

Another interesting result is the similarity in the mean level of water uptake by Scots pine at Svartberget and Åheden, despite differences between the sites. The

Fig. 7. The volume-weighted mean depth of water uptake for each tree as calculated from the three-source model of water uptake by trees. The best fit of the "original" values for the water sources are represented by open symbols. The average of the Monte Carlo simulations using isotope values from within the range of uncertainties are represented by solid symbols, and 1 SD in the range of depths returned by the Monte Carlo analysis is indicated by the vertical lines. The average simulated depth of water uptake by each species at each site is also plotted. Note that the average water uptake depth cannot be interpreted as the depth from which most water is taken up by trees.



coincidence of water uptake depth at the two sites may result from different influences. The competition from Norway spruce roots in superficial layers could be a factor at Svartberget, while the lower and less consistent availability of water in the superficial horizons may be a factor at Åheden, with its sandier soil and thinner mor layer.

Why and how different species take up water at different depths at different times of year is an intriguing question. It is, however, beyond the scope of this study to answer such questions. The ambition of this study was primarily to quantify the water uptake in the rooting zone without resorting to indirect hydrometric methods. Multiple hydrological tracers also provide a relatively inexpensive measure of root functionality, which can complement more time-consuming studies that map the distribution of roots. Thus, the most significant feature of this experiment is the demonstration of a method that lends itself for use as a routine complement to studies of plant–water relations and nutrient uptake.

That usefulness can be improved upon by using tree coring to remove the small amount of xylem sap required for isotope analysis without felling the tree. Tapping the tree can suffice with many deciduous tree species, but most conifers require extraction of xylem sap from the bole. Use of a safer artificial tracer, such as deuteriated water (^2H_2O) would also improve the method.

The usefulness of the technique must be judged not only by its simplicity, but also by the verisimilitude of the results. The Monte Carlo analysis of uncertainty in the definition of the model inputs indicated that the tracer signals were sufficiently strong to generate robust model results. The grouping of xylem sap compositions along the edges of the triangular source uptake diagram (Fig. 5) also suggests that two components can be sufficient to describe the distribution of water uptake in most trees on these sites. Thus, in this study, uncertainty stems more from the problem of precise identification of the isotopic "signature" of the three model water sources than a need for more water sources.

The isotopic signatures of different water sources should be both well characterized and distinctive, but those requirements tend to conflict. The quantification of water uptake below ca. 20 cm depth was hampered by the lower variation in the ^3H and $\delta^{18}O$ tracer signal at greater depths. This made the isotope signature of the deeper water easier to characterize, but reduced the precision with which the mixing model can apportion water uptake from deeper in the profile. On the other hand, the pronounced vertical gradient in both $\delta^{18}O$ and ^3H in the upper 2 dm of the soil makes the different superficial sources distinctive, but difficult to characterize without many samples. Considerable care, therefore, should be given to characterizing the tracer signal variation with depth. It should be remembered though, that while more intensive sampling can better define the vertical profiles of different traces, the separation of those profiles will entail a degree of subjectivity. The difficulty of circumventing this subjective element in selecting end members was discussed by Christophersen and Hooper (1992) in their study of the mixing model theory.

An alternative to compartmentalization is to define root uptake as a continuous function of depth, the parameters of which are then calibrated with the tracer information. Walker and Richardson (1991), for example, discuss the use of an exponential function of depth to model water uptake. The drawback to such a continuous function is the need to make an a priori assumption of a mathematical form for the vertical distribution of water uptake. In the case of using an exponential function of depth to describe the water uptake profile, there is an implicit assumption that there is an increase in water uptake towards the soil surface. While this assumption is a common one (Jansson and Halldin 1980), the results of this study contradict that assumption. Thus, while the compartmentalization involved in the three-component mixing model of water uptake is a simplification, it nonetheless provides a framework for interpreting the hydrological tracer data. Furthermore, this framework can utilize the extra information provided by a second (or more) independent tracers(s), as this study has demonstrated.

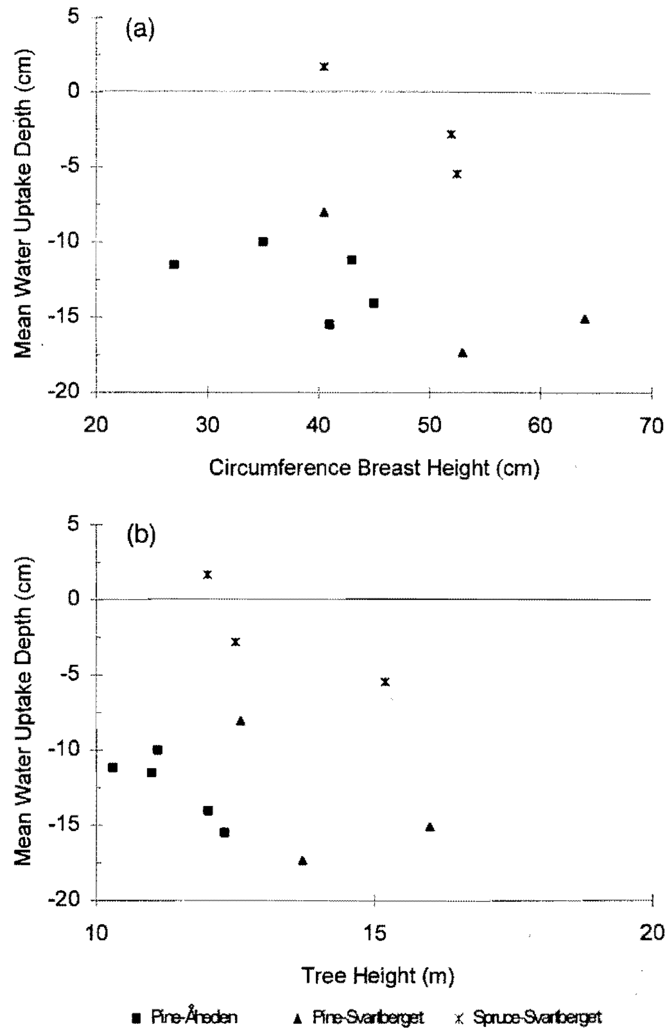
Conclusions

This study extends the application of hydrological isotope tracer methods to the problem of resolving the vertical distribution of water uptake by conifers in the upper decimeters of a podzolized forest soil. This was done using a three-source mixing model of xylem sap composition, where each source represents a different soil layer. To apply this three-source model, two independent hydrological tracers were needed. Those tracers were the naturally occurring vertical gradient of $\delta^{18}O$ in soil solution and a layer of ^3H inserted at the surface of the soil profile. Monte Carlo analysis of uncertainty indicated that the results of the mixing model were not unduly sensitive to the uncertainties in isotope analysis or the isotopic characterization of the three water sources.

This application demonstrated that most water uptake by Scots pine in the boreal study sites (one Scots pine only stand and one mixed Scots pine – Norway spruce stand) did not occur near the soil surface, where more than two-thirds of the fine roots were located, but rather a decimeter farther down in the soil profile. This suggests that the common assumption of a continuous decrease in water uptake with depth is not appropriate for Scots pine in the study area. The local increase in water content where the ^3H tracer was applied to the soil surface may have even resulted in an overestimate of the water uptake occurring in the superficial layers relative to the uptake if there had not been a disturbance caused by the experiment. In the mixed stand, the Norway spruce had a mean level of water uptake just 2 cm below the contact of the mor layer and mineral soil.

The nature of the information required for this mixing model of tree water uptake makes it particularly useful as a regular complement to studies of nutrient cycling where both soil solution and xylem sap are sampled. Care, however, must be taken to quantify and, in so far as possible, minimize the uncertainty in the analysis, much of which comes from defining the tracer concentrations in the different model water sources from which xylem sap water is taken up. Less disturbing methods for application of artificial tracers and removal of xylem sap would also be desirable.

Fig. 8. The relationship between the calculated mean depth of water uptake and the height (*a*) or circumference at breast height of the study trees (*b*). There is a tendency on each study site for circumference at breast height and height to increase with depth of water uptake in both Scots pine and Norway spruce. The greater size of the Scots pine at Svartberget relative to those at Åheden is a result of the more productive site quality at Svartberget.



Given the potential that trees have for selecting what is taken up from different portions of the root system, hydrological tracers can facilitate discrimination of passive and active nutrient uptake. The approach demonstrated here can also be used to study how various stresses, including pathogens, interspecific competition, drought, or acidification affect the distribution of functional roots within the soil. Advances in the use of inductively coupled plasma – mass spectrometry to routinely determine isotope ratios in a wide variety of components of soil solution will also open new possibilities for distinguishing the uptake of constituents besides water with the mixing model approach explored here.

Acknowledgments

The assistance of Benoit Pollier in the field was essential to the success of the work. Magnus Edström conducted the tedious centrifuge extractions with his customary good cheer. The reliable analysis of oxygen and tritium isotopes by Frank Westman and Rajinder Saxena from the Mass Spectrometry Laboratory at the Uppsala University Division of Hydrology was, as always, greatly appreciated.

References

Allison, G.B., Barnes, C.J., Hughes, M.W., and Leaney, F.W.J. 1984. Effect of climate and vegetation on oxygen-18 and deuterium profiles in soils. *In* Isotope Hydrology, 1983: Proceedings of an International Symposium on Isotope Hydrology in Water Resources Development, 12–16 Sept. 1983, Vienna. International Atomic Energy Agency, Vienna. pp. 105–122.

Bariac, T., Rambal, S., Jusserand, C., and Berger, A. 1989. Evaluating water fluxes of field-grown alfalfa from diurnal observations of natural isotope concentrations, energy budget and ecophysiological parameters. Agric. For. Meteorol. **48**: 263–283.

Bishop, K.H. 1991. Episodic increases in stream acidity, catchment flow pathways and hydrograph separation. Ph.D. thesis, Cambridge University, Cambridge, England.

Caldwell, M.M. 1976. Root extension and water absorption. *In* Water and plant life. *Edited by* O.L. Lange, L. Kappen, and E.D. Schulze. Ecol. Stud. **19**: 63–85.

Christophersen, N., and Hooper, R.P. 1992. Multivariate analysis of stream water chemical data: the use of principle components analysis for the end-member mixing problem. Water Resour. Res. **28**(1): 99–107.

Craig, H. 1961. Standard for reporting concentrations of deuterium and oxygen-18 in natural waters. Science (Washington, D.C.), **133**: 1833–1834.

Dambrine, E., Carisey, N., Pollier, B., and Granier, A. 1993. Effects of drought on the yellowing status and the dynamics of mineral elements in the xylem sap of declining spruce (*Picea abies* L.). Plant Soil, **150**: 303–306.

Dansgaard, W. 1964. Stable isotopes in precipitation. Tellus, **16**: 436–468.

Dawson, T.E. 1993 Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. Oecologia, **95**: 565–574.

Dawson, T.E., and Ehleringer, J.R. 1991. Streamside trees that do not use stream water: evidence from hydrogen isotope ratios. Nature (London), **350**: 335–337.

Ehleringer, J.R., and Dawson, T.E. 1992. Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ. **15**: 1073–1082.

Eriksson, B. 1986. The precipitation and humidity climate of Sweden during the vegetation period. Swedish Meteorological and Hydrological Institute, Stockholm. Rep. RMK 46.

Flanagan, L.B., Ehleringer, J.R., and Marshall, J.D. 1992. Differential water uptake of summer precipitation among co-occurring trees and shrubs in a pinyon–juniper woodland. Plant Cell Environ. **15**: 831–836.

Garnier, E., Berger, A., and Rambal, S. 1986. Water balance and pattern of soil water uptake in a peach orchard. Agric. Water Manage. **11**: 145–158.

Giesler, R., and Lundström, U. 1991. The chemistry of several podsol profile soil solutions extracted with centrifuge drainage technique. *In* Chemical weathering under field conditions. *Edited by* K. Rosén. Swedish University of Agricultural Science, Department of Soil Science, Uppsala. Rep. 63. pp. 158–165.

Glavac, V., Koenies, H., and Ebben, U. 1990. Seasonal variations in mineral concentrations in the trunk xylem sap of beech in a 42 year old beech forest stand. New Phytol. **116**: 47–54.

Granier, A., Biron, P., Köstner, B., Gay, L.W., and Najjar, G. 1995. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. Theor. Appl. Climat.

Jansson, P.-E., and Halldin, S. 1980. SOIL water and heat model. Technical description. Swedish coniferous forest project. Swedish Agricultural University, Uppsala. Tech. Rep. 26.

Kimmins, J.P., and Hawkes, B.C. 1978. Distribution and chemistry of fine roots in a white spruce – subalpine fir stand in British Columbia: implications for management. Can. J. For. Res. **8**: 265–279.

Kostler, J.N., Bruckner, E., and Bibelriether, H. 1968. Die wurzeln der Waldbaume. Verlag Paul Parey, Berlin.

Kramer, P.J., and Bullock, H.C. 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Am. J. Bot. **53**: 200–204.

Landsberg, J.J., and McMurtrie, R. 1984. Water use by isolated trees. Agric. Water Manage. **8**: 223–242.

Legge, N.J. 1985. Water movement from soil to root investigated through simultaneous measurement of soil and stem water potential in potted trees. J. Exp. Bot. **36**: 1583–1589.

Lu, P., Biron, P., and Granier, A. 1995. Water relations of adult Norway Spruce trees under soil drought in the Vosges mountains: water potential, stomatal conductance, and transpiration. Ann. Sci. For.

Majdi, H., and Persson, H. 1993. Spatial distribution of fine roots, rhizosphere and bulk-soil chemistry in an acidified *Picea abies* stand. Scand. J. For. Res. **8**: 147–155.

Nnyamah, J.U., and Black, T.A. 1977. Rates and patterns of water uptake in a Douglas-fir forest. Soil Sci. Soc. Am. J. **41**: 972–979.

Nordén, L.-G. 1989. Water use by Norway spruce. Ph.D. thesis, Swedish University of Agricultural Sciences, Umeå.

Nordén, L.-G. 1990. Depletion and recharge of soil water in two stands of Norway spruce. Hydrol. Processes, **4**(3): 197–213.

Penman, H.L. 1963. Vegetation and hydrology.

Commonwealth Agricultural Bureau, Farnham Royal, England. Tech. Commun. 53.

Rodelli, M.R., Gearing, J.N., Gearing, P.J., Marshall, N., and Sasekumar, A. 1984. Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. Oecologia, **61**: 326–333.

Saxena, R. 1987. Oxygen-18 fractionation in nature and estimation of groundwater recharge. Ph.D. thesis, Uppsala University, Uppsala, Sweden. UNGI Rep. Ser. A. No. 40.

Thorburn, P.J., and Walker, G.R. 1993. The source of water transpired by *Eucalyptus camaldulensis*: soil, groundwater, or streams. *In* Stable isotopes and plant carbonwater relations. *Edited by* J.R. Ehleringer, A.E. Hall, and G.D. Farquhar. Academic Press, San Diego, Calif. pp. 511–527.

Thorburn, P., Walker, G., and Hatton, T. 1992. Are river red gums taking water from soil, groundwater or streams? *In* Catchments of Green, National Conference on Vegetation and Water Management, Adelaide. pp. 37–42.

Thorburn, P., Walker, G., and Brunel, A. 1993. Extraction of water from *Eucalyptus* trees for analysis of deuterium and oxygen-18: laboratory and field techniques. Plant Cell Environ. **16**: 269–275.

Walker, C.D., and Richardson, S.B. 1991. The use of stable isotopes of water in characterising the source of water in vegetation. Chem. Geol. **94**: 145–158.

Wershaw, R.L., Friedman, I., and Heller, S.J. 1966. Hydrogen isotope fractionation of water passing through trees. *In* Advances in organic geochemistry. *Edited by* G.D. Hobson and G.C. Speers. pp. 55–67.

White, J.W.C. 1988. Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 142–162.

White, J.W.C., Cook, E.R., Lawrence, J.R., and Broecker, W.S. 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. Geochim. Cosmochim. Acta, **49**: 237–246.